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# Experimental comparison of competition and facilitation in alpine communities varying in productivity

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## Abstract

**Question.** Competitive and facilitative interactions among plant species in different abiotic environments potentially link productivity, vegetation structure, species composition and functional diversity. We investigated these interactions among four alpine communities along an environmental productivity gradient in a generally harsh climate. We hypothesised that the importance of competition would be higher in more productive sites.

**Location.** Mt. M. Khatipara (43°27'N, 41°41'E, altitude 2750 m), NW Caucasus, Russia. Communities ranged from low-productivity alpine lichen heath (ALH) and snowbed communities (SBC), to intermediate productivity *Festuca* grassland (FVG), and high-productivity *Geranium-Hedysarum* meadow (GHM).

**Methods.** We quantified the relative influence of competition and facilitation on community structure by expressing biomass of target species within each natural community proportionally to biomass of the species in a “null community” with experimental release from interspecific competition by removing all other species (for 6 years). An overall index of change in community composition due to interspecific interactions was calculated as the sum of absolute or proportional differences of the component species.

**Results.** Species responses to neighbour removal ranged from positive to neutral. There was no evidence of facilitation among the selected dominant species. As expected, competition was generally most important in the most productive alpine community (GHM). The intermediate position for low-productivity communities of stressful environments (ALH, SBC) and the last position of intermediately productive FVG were unexpected.

**Conclusions.** Our results appear to support the Fretwell-Oksanen hypothesis in that competition in communities of

intermediate productivity was less intense than in low- or high-productive communities. However, the zero net effect of competition and facilitation in FVG might be the result of abiotic stress due to strong sun exposure and high soil temperatures after neighbour removal. Thus, non-linear relationships between soil fertility, productivity and different abiotic stresses may also determine the balance between competition and facilitation.

**Keywords:** Alpine lichen heath; Fretwell-Oksanen hypothesis; Neighbour removals; Null community; Snowbed community.

**Nomenclature:** Vorob'eva & Onipchenko (2001)

## Introduction

The relative importance of competitive and facilitative interactions among plant species in different abiotic environments is hotly debated in the literature, because it could link productivity, vegetation structure, species composition and functional diversity (Tilman 1988; Grace 1993; Grime 2001; Hooper et al. 2005), and has been the subject of extensive experimental research (Wedin & Tilman 1993; Bonser & Reader 1995; Kadmon 1995; Callaway & Walker 1997; Gigon 1999; Goldberg et al. 1999; Mulder et al. 2001; Suding et al. 2004; van Ruijven & Berendse 2005; Wardle & Zackrisson 2005; Gross et al. 2007). Both competition and facilitation play important roles in the organization of alpine plant communities, which are generally exposed to harsh climates (del Moral 1983; Carlsson & Callaghan 1991; Egerton & Wilson 1993; Callaway

1995; Kikvidze 1996; Theodose & Bowman 1997; Aksenova et al. 1998; Choler et al. 2001; Kikvidze et al. 2001; Callaway et al. 2002; Olofsson 2004; Onipchenko 2004; Dullinger et al. 2007). However, it is difficult to estimate the relative roles of these interactions in forming the structure of specific communities, especially under natural conditions over a period of many years. For studying such interactions, experimental species removal can be a powerful tool, for which two specific approaches have been followed. Most emphasis has been on the first approach, in which only one dominant species or plant functional type is removed from a natural community (Aksenova et al. 1998; Diaz et al. 2003; Bret-Harte et al. 2004; Suding et al. 2006). This has provided important insights into the different roles of individual species or functional types within their community.

Goldberg (1994) suggested a second approach for determining the contribution of species interactions, especially competition, to community structure. This method entails comparing species biomass within a community with biomass of a so-called “null community”, where species are represented proportionally to their biomass in monocultures. In other words, a species is experimentally released from competition. When we remove all species except one from sampling plots, we can observe the net “community effect” on the target species. This removal approach is opposite to the first proposal, in that it principally provides information about the net effect of competitive and/or facilitative interactions of a community. If competition is more important, the abundance of the species should increase after removal of its neighbours. If facilitation dominates, the abundance of the target species should decrease. Removal of neighbours may answer the question of whether there is an advantage or disadvantage to a species of growing within a community as opposed to growth in isolation (monoculture). We hypothesise less response to neighbour removal around a dominant species than around a subordinate species because, in the case of a target dominant species, the absolute and relative biomass removal around it will be less.

Our study addresses the influence of interactions among plant species on community structure along a mesotopographical gradient in the temperate alpine landscape of Teberda Nature Reserve in the Northwest Caucasus. The alpine plant communities at Teberda are convenient objects for experimental research on the structuring of plant communities because they are essentially pristine and exhibit great variability in productivity and

environmental conditions within a small area (Onipchenko 2004). This research reports the results of a large, long-term vegetation removal experiment. It compares the responses of four dominant plant communities, focussing on two main questions: (1) What is the net interaction effect of an alpine plant community on different common alpine species? (2) How do the roles of competition and facilitation change among communities along an environmental productivity gradient under a generally harsh alpine climate? We tested the specific hypothesis that the importance of interspecific competition would increase with productivity. This is, to our knowledge, the first time that long-term community-level vegetation removal has been applied to test for the importance of competition along environmental gradients.

## Materials and Methods

### *Study area and communities*

The study area is in the Teberda State Nature Reserve (*Teberdinskii zapovednik*) in the Karachaevo-Cherkessia Republic in the Northwest Caucasus, Russia. Study sites are located on Mount Malaya Khatipara (43°27'N, 41°41'E), in the alpine zone at 2700–2800 m a.s.l. This area has a temperate mountain climate, type X(VI) according to Walter et al. (1975). The mean annual temperature is  $-1.2^{\circ}\text{C}$  and mean annual precipitation is 1400 mm. The warmest month is August, with a mean monthly temperature of  $+8.3^{\circ}\text{C}$ , but frost can occur at any time during the summer. Southerly winds dominate, so south-facing slopes are exposed and largely snow-free, whereas north-facing slopes are leeward, with heavy snow accumulation.

Siliceous rocks (biotite, granite) are the most common type in the study area (Grishina et al. 1993). The soils are acidic, rich in organic matter and available potassium, but have low mobile nitrogen and phosphorus content. Ammonium and humus content, and therefore soil fertility, increase along the snow gradient (Table 1).

Snow accumulation is the main factor controlling the vegetation pattern of the area (Onipchenko 1994). Four alpine communities arranged along the local snow gradient from essentially snowless to snowiest were included in this study: (1) Alpine lichen heath (tundra) dominated by fruticose lichens (ALH); (2) *Festuca varia* grassland (FVG); (3) *Geranium gymnocaulon*-*Hedysarum caucasicum* meadow (GHM); and (4) the snowbed community

**Table 1.** Selected properties of studied alpine communities. ALH – alpine lichen heath, FVG – *Festuca varia*-dominated grassland, GHM – *Geranium gymnocaulon*–*Hedysarum caucasicum*-dominated meadow, SBC – snowbed community (after Onipchenko 1994).

Community	ALH	FVG	GHM	SBC
Aspect	S	SSW	SW	SW
Average slope (degrees)	15	10	5	1
Depth of winter snow cover (m)	0–0.3	0.5–1.5	1.5–3	> 3
Vegetative season (months)	4.5–5.5	3.5–4.5	2.5–3.5	2.0–2.5
Biomass (g/m <sup>2</sup> ): aboveground	110 ± 7	307 ± 17	319 ± 20	129 ± 5
Belowground	478 ± 42	636 ± 34	1392 ± 177	944 ± 128
Annual production (g/m <sup>2</sup> )	150	400	550	200
Zoogenic soil disturbance (vole burrows)	Weak	Medium	Strong	Weak
Depth of humus layer (cm)	15–20	20–24	19–22	16–17
Stone content in soil (0–10 cm, volume %)	13	10	9	5
Humus store in the 0–40 cm (kg/m <sup>2</sup> )	15.6	19.6	23.0	32.5
Available nutrients in the upper soil layer (mg/100 g):				
N(NH <sub>4</sub> )	1.2	3.2	4.2	6.1
P	0.6	0.5	0.8	0.7
K	29	19	31	61

(SBC) (Table 1). For a detailed description of the area, soil and vegetation types, see Onipchenko (1994, 2002, 2004). Biomass and productivity data for these communities are provided in Table 1.

Alpine lichen heaths (ALH) (phytosociological association: *Pediculari comosae-Eritrichietum caucasicum oxytropidetosum kabanensis* Minaeva et Onipchenko 2002, in Onipchenko 2002) are low-productivity communities with fruticose lichens as the main dominants (mostly *Cetraria islandica* (L.) Ach.). They occupy windward crests and slopes. The snowpack in winter is shallow or practically absent. Soils freeze deeply and have high stone content. The growing season lasts for over 5 months.

Grasslands dominated by *Festuca varia* (FVG) (*Viola altaicae-Festucetum variaie* Rabotnova et Onipchenko, in Onipchenko 2002) are firm-bunchgrass communities with high litter accumulation in the aboveground layer. FVGs are floristically rich, medium-productive, and are similar to low-elevation steppe in many characteristics (Onipchenko & Semenova 1995).

Meadows dominated by the forbs *Geranium gymnocaulon* and *Hedysarum caucasicum* (GHM) (*Hedysaro caucasicum-Geranieta gymnocauli* Rabotnova et Onipchenko 2002, in Onipchenko 2002) are the most productive alpine community in the area. They develop on sites with considerable snow accumulation and a growing season of only 2.5 to 3 months.

Alpine snowbed communities (SBC) (*Hyalopoo ponticae-Pedicularietum nordmannianae* Rabotnova et Onipchenko, in Onipchenko 2002) are low productive. They occupy depressions and bottoms of nival and glacial corries with heavy winter snow accumulation. Short rosette and dwarf clonal plants

(*Gnaphalium supinum*, *Sibbaldia procumbens*, *Taraxacum stevenii*) dominate the snowbeds. The growing season is the shortest of the four communities (about 2–2.5 months).

#### Target species

It was not possible to investigate all species of the above communities. We chose four vascular species (dominants, as well as selected common subdominant species) from each of FVG, GHM, SBC and six species from ALH, due to the polydominant structure of the latter. These species (see Table 2) together constitute at least two-thirds of the aboveground biomass of each of the communities. Most of the species belong to Asteraceae (six species) and Poaceae (four species), while Fabaceae was represented by two species, and all other families were represented by a single species (Table 2).

#### Field experimental design

The field experiment began in 1995 and the final harvest was carried out in 2001. Eight circular experimental and control plots were established for each studied species in the natural alpine setting inside the nature reserve. Plots were paired: each control plot was near (< 1 m from) an experimental plot. The control and experimental plots were chosen to be as similar as possible by visual inspection of initial structure and composition. Plots were marked with aluminium wire. Owing to different plant sizes, which were assumed to correspond to the spatial scale of plant-plant interactions, we used three plot sizes (Table 2). All aboveground biomass of vascular plants, except the target species, was

**Table 2.** List of studied species and their plot size (nomenclature according to Vorob'eva & Onipchenko 2001).

Community	Species	Family	Plot diameter (cm)
ALH	<i>Anemone speciosa</i> Adams ex G.Pritz.	Ranunculaceae	29
	<i>Campanula tridentata</i> Schreb.	Campanulaceae	20
	<i>Antennaria dioica</i> (L.) Gaertn.	Asteraceae	20
	<i>Trifolium polyphyllum</i> C.A.Mey.	Fabaceae	29
	<i>Carex</i> spp. ( <i>C. umbrosa</i> Host, <i>C. sempervirens</i> Vill., <i>C. caryophyllea</i> Latourr.)	Cyperaceae	20
	<i>Festuca ovina</i> L.	Poaceae	20
FVG	<i>Scorzonera cana</i> (C.A.Mey.) O.Hoffm.	Asteraceae	29
	<i>Festuca varia</i> Haenke	Poaceae	49
	<i>Nardus stricta</i> L.	Poaceae	29
	<i>Leontodon hispidus</i> L.	Asteraceae	49
GHM	<i>Geranium gymnocaulon</i> DC.	Geraniaceae	49
	<i>Hedysarum caucasicum</i> Bieb.	Fabaceae	49
	<i>Matricaria caucasica</i> (Willd.) Poir.	Asteraceae	29
	<i>Phleum alpinum</i> L.	Poaceae	29
SBC	<i>Minuartia aizoides</i> (Boiss.) Bornm.	Caryophyllaceae	20
	<i>Taraxacum stevenii</i> DC.	Asteraceae	20
	<i>Sibbaldia procumbens</i> L.	Rosaceae	20
	<i>Gnaphalium supinum</i> L.	Asteraceae	20

completely and carefully removed from the experimental plots using scissors. This clipping procedure was repeated several times in 1995 and in all subsequent years. Such periodic clipping has a minimal impact on the soil and mycorrhizal network (McLellan et al. 1997), although we cannot entirely exclude the possibility of other experimental artefacts, e.g. increased nutrient mineralization linked to root death of some species. Roots were cut around the periphery of the experimental plots every 2 years to prevent root competition with the surrounding vegetation. The size of the plots was adequate to eliminate aboveground competition for light with neighbouring vegetation and to leave a small buffer around each plot to mitigate possible side effects. Shoot number and plant size for each target species was estimated each year from 1995 to 2001, but these parameters are not considered in the present paper. Here, we focus on the aboveground biomass measurements estimated during the summer of 2001 on experimental and control plots. Dry plant mass was determined after drying for 8 h at 105°C.

#### Statistical analysis

The influence of neighbour removal on target plant biomass was estimated using one-way ANOVAs. To compare the role of competition or facilitation in the studied alpine communities, the following indices were calculated (Goldberg 1994).

The expected relative abundance of species *i*:

$$RY_{im} = Y_{im} / \Sigma Y_{im},$$

where  $Y_{im}$  = the final abundance (aboveground biomass in our case) of species *i* in monoculture, and

$\Sigma Y_{im}$  = the sum of abundances of all the separate monocultures.

The actual relative abundance in mixture (natural community in our case) was calculated as

$$RY_{ix} = Y_{ix} / \Sigma Y_{ix},$$

where  $Y_{ix}$  = the final abundance (aboveground biomass in our case) of species *i* in control plots of studied alpine communities, and  $\Sigma Y_{ix}$  = the sum of abundances of all the control community plots. Due to different plot sizes in the field experiment,  $RY_{im}$  and  $RY_{ix}$  were calculated after dividing biomass values for medium plots (diameter 29 cm) by two, and for large plots (diameter 49 cm) by six, in order to match the biomass to that in the smaller (20 cm diameter) plots. Absolute (*D*) and proportional differences (*PD*) in relative abundance were calculated as:

$$D_i = RY_{ix} - RY_{im}$$

$$PD_i = (RY_{ix} - RY_{im}) / RY_{im}$$

An overall index of change in community composition due to interspecific interaction was calculated as the sum of absolute values of the difference or proportional difference:

$$D = \Sigma |D_i|$$

$$PD = \Sigma |PD_i|$$

These indices are dependent on the number of studied species. Therefore, we divided values for ALH (six species against four in the other communities) by 1.5. Goldberg (1994) noted that "the sum of proportional differences (*PD*) in relative abun-

dance due to species interaction is much more sensitive to changes in rare species than is the sum of absolute differences ( $D$ )."

## Results

### *Species responses*

Species response to neighbour removal was either positive (target species biomass increased, suggesting better growth in the absence of competition) or neutral (no significant change in above-ground biomass) (Fig. 1). There were no cases with a significant negative reaction to the removals, i.e. there was no evidence of net facilitation of the target species.

Three of six studied species of ALH increased their biomass significantly after neighbour removals (*Antennaria dioica*, *Campanula tridentata*, *Festuca ovina*). For the first two species, aboveground biomass on experimental plots was more than twice that on the control plots after 6 years of clipping. *Anemone speciosa* and *Carex* spp. showed no response, while *Trifolium polyphyllum* showed an upward trend in experimental plots.

None of the four studied species of FVG changed their biomass significantly after 6 years of neighbour removal, although *Nardus stricta* showed a negative trend.

GHM species demonstrated a more complex response to species removal. Neither of the two main dominants (*Hedysarum caucasicum*, *Geranium gymnocaulon*) changed their biomass significantly, although *H. caucasicum* had a modest upward trend. Two subdominants, *Matricaria caucasica* and *Phleum alpinum*, increased in abundance by 2.5-3.0-fold on experimental plots in comparison with the control. This is evidence of competitive release in the absence of main dominants.

All studied species in SBC at least doubled their biomass after neighbour removals, although for *Minuartia aizoides* and *Sibbaldia procumbens* this response was just below the significance level. The biomass of *Gnaphalium supinum* on experimental plots was more than five times that in the control plots.

The overall response patterns of alpine species to neighbour removal differed within and between communities. We observed stronger reactions for subordinate than for dominant species in the most productive community, *Geranium-Hedysarum* meadow, and in the second lowest producing snowbed community. Correlation coefficients between above-

ground biomass on control plots and  $D_i$  or  $PD_i$  were significantly positive for eight species of these communities (0.87 and 0.81 correspondingly,  $n = 8$ ,  $P = 0.005$  and  $0.016$ ). Less abundant species were more suppressed by competition than were dominants.

### *Comparison among communities along the environmental gradient*

We calculated absolute ( $D$ ) and proportional differences ( $PD$ ) in relative abundance in monoculture and control communities for the studied species (Table 3). We then ranked (Table 4) the communities according to these indices:

$$D : FVG < ALH < SBC < GHM$$

$$PD : FVG < SBC < ALH < GHM$$

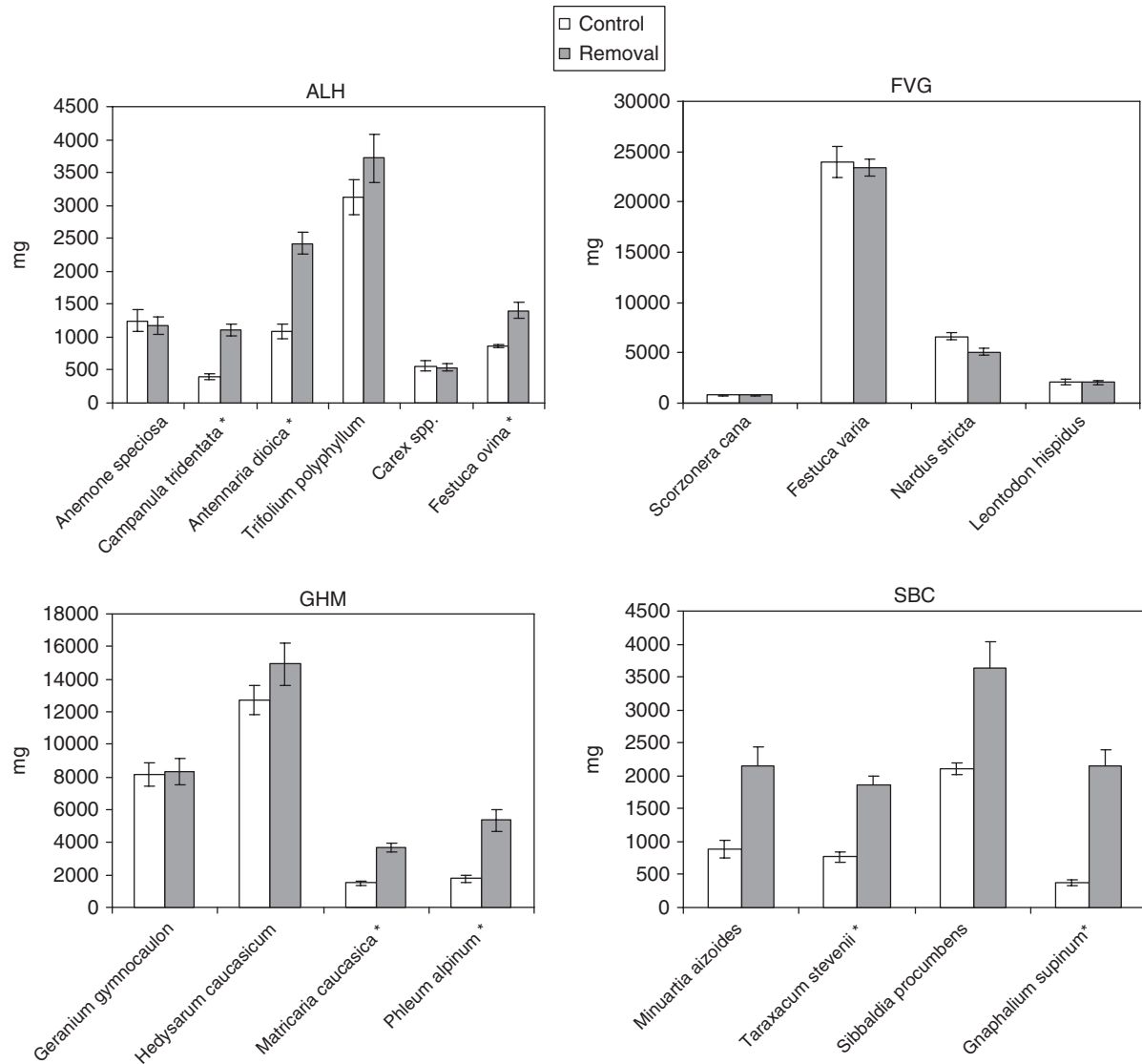
In general, the importance of competition in the communities increased in the order: FVG < ALH, SBC < GHM.

## Discussion

To our knowledge, this is the first time that the importance of competition along environmental gradients has been quantified using long-term community-level vegetation removal experiments. Competitive and neutral relationships among plants were dominant in the four alpine communities. As expected, competition was more important in the most productive alpine community (*Geranium-Hedysarum* meadow, GHM). However, the intermediate response to complete neighbour removal for low-productive communities in stressful environments (alpine lichen heath and snowbed communities) and the weakest response in the medium-productive *Festuca varia* grassland did not support our hypothesis. Below, we discuss some factors that may help to explain these unexpected findings.

### *Competition versus facilitation and abundance response versus biomass response*

Given the dominance of competitive interactions in the four alpine communities, neutral relationships among species may have reflected the net balance between positive (facilitative) and negative (competitive) relations rather than absence of interspecific interactions. The lack of overall facilitation in any of our communities is surprising,



**Fig. 1.** Influence of neighbour species removal on aboveground biomass of target species (mean  $\pm$  standard error,  $n = 8$ ). \*Difference significant at  $P < 0.05$  as tested with one-way ANOVA.  $df = 1$ .  $df$  error = 14).

given the harshness of the climate. However, similar results were obtained by Kikvidze et al. (2001) for subalpine meadows in the Central Caucasus and by Olofsson et al. (1999) and Klanderud & Totland (2005) for harsh arctic communities in Norway.

An earlier paper using species removal (Aksenova et al. 1998) found evidence for both competition and facilitation in alpine lichen heath (ALH). In terms of competition, our results are consistent with Aksenova et al. (1998), who found positive responses for *Antennaria dioica*, *Festuca ovina* and *Trifolium polyphyllum* to reciprocal removals, while *Anemone speciosa* was generally unresponsive in both studies. This long-lived species lacks stolons and depends on seed for reproduction. Thus it is

likely to be the least responsive to any change in this community (Aksenova et al. 2004). *Carex* spp. showed a moderately positive response to the removal of *Festuca ovina* in the earlier study, but we did not observed any response at all.

Aksenova et al. (1998) found that *Campanula tridentata* showed a pronounced negative response to the removal of the clover *Trifolium polyphyllum* and moderately negative responses to removal of *Antennaria dioica*, *Anemone speciosa* and *F. ovina* in alpine lichen heath. These results suggest facilitation and contradict the outcome of the current study, in which *C. tridentata* actually showed a significant positive biomass response when grown in monoculture. The key to resolving this paradox is in the measurement

**Table 3.** Relative abundance of species in monoculture ( $R_{im}$ ) and control communities ( $R_{ix}$ ) and absolute ( $D_i$ ) and proportional difference ( $PD_i$ ) in relative abundance between monoculture and control communities.

Community	Species	$R_{im}$	$R_{ix}$	$D_i$	$PD_i$
ALH	<i>Anemone speciosa</i>	0.074	0.122	0.048	0.648
ALH	<i>Campanula tridentata</i>	0.140	0.078	-0.062	-0.441
ALH	<i>Antennaria dioica</i>	0.306	0.214	-0.092	-0.300
ALH	<i>Trifolium polyphyllum</i>	0.234	0.307	0.072	0.309
ALH	<i>Carex</i> spp.	0.068	0.110	0.042	0.615
ALH	<i>Festuca ovina</i>	0.177	0.169	-0.009	-0.049
FVG	<i>Scorzonera cana</i>	0.050	0.046	-0.004	-0.087
FVG	<i>Festuca varia</i>	0.496	0.457	-0.039	-0.078
FVG	<i>Nardus stricta</i>	0.323	0.378	0.055	0.172
FVG	<i>Leontodon hispidus</i>	0.132	0.119	-0.013	-0.095
GHM	<i>Geranium gymnocaulon</i>	0.165	0.266	0.101	0.611
GHM	<i>Hedysarum caucasicum</i>	0.297	0.416	0.119	0.401
GHM	<i>Matricaria caucasicum</i>	0.219	0.145	-0.074	-0.339
GHM	<i>Phleum alpinum</i>	0.318	0.173	-0.146	-0.458
SBC	<i>Minuartia aizoides</i>	0.221	0.215	-0.005	-0.024
SBC	<i>Taraxacum stevenii</i>	0.190	0.185	-0.005	-0.026
SBC	<i>Sibbaldia procumbens</i>	0.370	0.509	0.138	0.373
SBC	<i>Gnaphalium supinum</i>	0.219	0.091	-0.128	-0.585

**Table 4.** Sum of absolute ( $D$ ) or proportional difference ( $PD$ ) in relative species abundance for the studied communities.

Index	ALH	FVG	GHM	SBC
$D$	0.216	0.111	0.440	0.276
$PD$	1.574	0.432	1.808	1.008

chosen to estimate plant performance. When only biomass is used (as in our study), a change in the total number of vegetative or generative shoots may go unnoticed. *C. tridentata* has been shown to have a high proportion of juvenile individuals in its population (Onipchenko & Komarov 1997). When other dominants are removed, young unsheltered *C. tridentata* plants respond negatively, while the adults respond positively. The disappearance of many small juvenile shoots is more than compensated for by an increase in biomass of fewer but much larger adults. A comparable difference in pattern for shoot density versus vegetation cover has also been reported in the context of seed size-plant abundance relationships (Murray et al. 2005).

The differences in response to neighbour removal for shoot abundance and biomass were also evident in the GHM community. For example, nine out of 16 species responded positively to the individual removal of *Geranium gymnocaulon*, *Hedysarum caucasicum*, or both, in an earlier ex-

periment by Cherednichenko (2004). As in our study, *H. caucasicum* responded positively to the removal of its main competitor *G. gymnocaulon*. The other species common to both studies, *Matricaria caucasicum*, showed a significant increase in biomass in this study when growing in monoculture (evidence of competition), but a decrease in the number of individual shoots in Cherednichenko's (2004) study when *Geranium* alone or *Geranium* and *Hedysarum* were removed (evidence of facilitation). However, when only *Hedysarum* was removed, *Matricaria* showed an increase in shoot numbers (evidence of competition). We need to stress that in her study only juvenile plants of *M. caucasicum* were found, so again, as in the ALH example above, different parts of the life cycle of this plant may exhibit prevalence of competitive exclusion for adults and sheltering effects for the juveniles. After 9 years of the dominant removal experiment, *Geranium* did not increase its aboveground biomass after *Hedysarum* removal, as in our experiment (A.A. Akhmetzhanova, personal communication). As hypothesised, the dominant did not show a positive response due to relatively low availability of additional resources after subordinate species removals. Indeed, biomass of the subordinate *M. caucasicum* increased significantly after *Geranium* removal (A.A. Akhmetzhanova, personal communication), in concordance with our results. The same tendency was observed in dry meadows in NW Switzerland (Gigon & Marti 1994; Marti 1994).

The main dominants of *Festuca varia* grassland (FVG: *Festuca varia*) and snowbed communities (SBC: *Sibbaldia procumbens*) did not respond to removal of other dominants (*Nardus stricta* and *Taraxacum stevenii*) in the corresponding communities (Elumeeva 2004; Bidzhieva 2005). In our experiment, *F. varia* did not increase, but *S. procumbens* did increase after removal of all neighbours. These results may be explained by the differences in proportions of the species in the aboveground biomass: 57% for *Festuca* in FVG, but only 39% for *Sibbaldia* in SBC. So again, as hypothesised, the proportion of biomass removal of neighbour plants mattered to the response of the target species. Similar results were obtained by Bonser & Reader (1995) for *Poa compressa* – the more plant biomass that was removed from around it, the better its observed growth.

#### *Productivity and competition in different communities*

Overall, we did not find a linear positive relationship between overall competition strength and



productivity (or biomass) in the studied communities. Less productive communities (ALH, SBC) were intermediate in terms of competition. When ranked by annual production of aboveground biomass (Onipchenko 2004), the communities were arranged as follows ( $\text{g} \cdot \text{m}^{-2}$  per year in parentheses):

GHM(550) > FVG(400) > SBC(200) > ALH(150)

When adjusted for the length of the vegetative season (Körner 1999), which ranges from 5 months in ALH to 2.25 months in SBC, the sequence remained the same, but there was a more apparent difference in productivity between SBC and ALH in  $\text{g} \cdot \text{m}^{-2}$  per growth month:

GHM(183) > FVG(100) > SBC(89) > ALH(30)

So, FVG and SBC are more similar to each other in terms of monthly productivity. The most productive community, whether ranked by annual or growing season-adjusted biomass, was indeed the one that was most influenced by competition. Indeed, GHM had the most consistent and strongest positive response, as measured by the proportional or absolute difference in relative abundance of constituent species between the original community and the monoculture. The greater role of competition under more productive conditions was also demonstrated in experimental neighbour removal around *Hieracium floribundum* (Reader 1990) and around *Anthoxanthum odoratum* (Sammul et al. 2000).

Competition is pronounced in SBC but less so in ALH. However, as explained above, the weakest removal response is observed not in the least productive ALH, but in the second most productive FVG. Similarly, Goldberg calculated D and PD indices for Campbell & Grime's (1992) data and concluded that, "both indices of species composition tend to show the least effect of competition at intermediate nutrient levels" (Goldberg 1994; see p. 1504). The explanation for this pattern may lie not only in differences in productivity – and possible differences in herbivory regimes. FVG is characterized by high sunlight exposure on steep south-facing slopes leading to high temperatures and soil drought. Here, plants that shelter each other may experience more favourable conditions in mixtures than when grown alone. Thus, it appears that the neutral balance between competition and facilitation in FVG is the result of abiotic stress upon neighbour removal. Thus, non-linear relationships between soil fertility and productivity and different abiotic stresses may also determine the balance between competition and facilitation.

## Conclusion

Our results support neither the hypothesis that competition has stronger effects on species composition in more productive communities (Grime 1977, 2001), nor the alternative hypothesis that the effects of competition on species composition do not change over productivity gradients (Tilman 1988). However, our results are similar to those obtained by Goldberg (1994). With an added caveat for possible, yet unknown, effects of any experimental (belowground) artefacts, our results seem to support the Fretwell-Oksanen hypothesis (Fretwell 1977, 1987; Oksanen et al. 1981) that competition in communities of intermediate productivity has stronger effects on biomass structure than in low- or high-productivity communities. However, we need further in-depth experiments to investigate the possibility that abiotic factors other than those directly controlling productivity may provide an alternative explanation for this pattern.

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